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論文題目	Community assembly and dynamics in tropical rainforests on the basis of functional traits（機能形質にもとづいた 熱帯雨林の群集形成と群集動態）
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Chapter 1: Effects of habitat filtering and negative density dependence on community dynamics in a tropical rainforest

While numerous hypotheses have been proposed to explain patterns of diversity in plant communities, less is known about their relative contributions to community assembly and dynamics. I hypothesized that tree survival rate showed bell-shaped response to local conspecific density, because they suffer stronger effect of habitat filtering (HF) when they are rare and stronger effect of negative density dependence (NDD) when they are abundant in local communities. I tested this hypothesis by using individual-level regression of 618 tree species in the 52-ha Lambir Forest Dynamics Plot (FDP; Lambir Hills National Park, Sarawak, Malaysia). Combined all species, I found a significant negative quadratic relationship between survival rates and both local conspecific and heterospecific density. Negative conspecific density effect works on 87% of individuals in the FDP, and the rest of individuals showed positive density effects of conspecific density. On the other hand, positive heterospecific density effect works on 99% of individuals in the FDP. When I distinguished two types of survival rates response of each species based on the median of conspecific density and peak: HF species (the median of conspecific density is smaller than the conspecific density of the peak) and NDD species (the median of conspecific density is larger than the conspecific density of the peak), NDD species had significantly larger species abundance at the 52-ha scale. These results suggest that HF control survival rates more broadly than NDD does in the FDP. However, this does not mean NDD is less important than HF in structuring a community. As NDD works on individuals with high conspecific density and abundant species in the FDP, my results highlight the role of NDD in maintaining the diversity of species-rich tropical forest.

Chapter 2: Soil resource availability shapes community trait structure in a species-rich dipterocarp forest

Habitat filtering and limiting similarity have been proposed as two opposing forces structuring community memberships. Community assembly theory proposes habitat filtering as a mechanism restricting community membership according to the ecological strategies of species in a given environment. Limiting similarity posits that some species exclude others that are ecologically similar. I quantified nine ecophysiological and life-history traits for 80 dipterocarp species in the 52-ha Lambir Forest Dynamics Plot (FDP; Lambir Hills National Park, Sarawak, Malaysia). I studied forests on four soil types differing in fertility and moisture, focusing on soil resource availabilities as environmental determinants of habitat filtering processes. I used a

null-model approach to detect the strengths of habitat filtering and limiting similarity. I quantified the relative contributions of soil resources (nutrients and water) to habitat filtering by comparing the strength of habitat filtering processes (i.e. effect sizes) at the overall plot scale and at the individual soil-type scale. I also compared the strengths of assembly processes among soil types. Compared to a null model at micro-scale ($20 \times 20\text{m}$), trait range and variance were reduced for seven out of nine functional traits, suggesting the importance of habitat filtering in the dipterocarp community. I also found a broader distribution of five traits, and more even spacing for seven traits ($20 \times 20\text{m}$), which is consistent with the concept of limiting similarity. Randomisations which swapped species occurrences within soil types (i.e. null models removing soil effects in assembly processes) were much closer to observed values and there were no phylogenetic constraints on habitat association. Hence, soil resource availability acted as a habitat filtering mechanism in the FDP; relative contributions to habitat filtering ranged from 35% for seed mass to 77% for relative growth rate. Furthermore, soil types apparently affected the strengths of habitat filtering and limiting similarity. I demonstrate that soil resource availability is a crucial determinant of habitat filtering in this species-rich tropical rainforest; the strengths of assembly processes differed among soil types. Variation in soil resource availability can shape the distribution of traits through community assembly processes, promoting trait diversification and species coexistence.

Chapter 3: Nonrandom abundance distributions of a tropical rain forest tree community: evidence from the patterns of traits correlation at a local scale

Community assembly theory proposes habitat filtering as a mechanism restricting community membership according to the ecological strategies of species in a given environment. Most studies using trait distributions are based on species presence/absence data and do not incorporate relative species abundance. I conducted a critical test of neutral and niche based species abundance distribution theories based on a community aggregated trait values of a dipterocarp community in the 52-ha Lambir Forest Dynamics Plot (FDP; Lambir Hills National Park, Sarawak, Malaysia) where approximately 80 species of dipterocarp trees co-occur. I expected the observed community mean traits weighted by abundance should be stronger than an abundance neutral model predicted. The key assumption of this approach is that habitat filtering leads to strong correlations between community mean traits. First, I constructed a simulation model of community assembly to examine habitat filtering led strong correlations between community mean traits. I found that correlations of community mean traits are generally significantly

stronger under habitat filtering simulations than those produced by random assembly simulations. However, two out of ten pairs of functional traits did not distinguish habitat filtering assembly and random assembly. Then, using null model approaches, I quantified the strength of correlations of community mean traits weighted by the actual abundance in the FDP. I found relationship among community mean traits of dipterocarp trees were generally stronger than expected by the random assembly and abundance neutral expectations, suggesting that habitat filtering determines not only species membership in local communities but also species abundance. When I restricted the analysis to adult trees, the strength of relationship among each community mean trait was close to abundance neutral expectations and consistent with a pattern of negative density dependence. These results suggest that: (1) highly nonrandom and deterministic processes, namely habitat filtering and negative density dependence, shape species abundance distribution within local communities in this species-rich tropical rain forest; and (2) the use of simulations to validate null models is imperative before any ecological explanations are offered to observed trait distributions.

論文審査結果の要旨

生物群集のパターンとそれを生み出す機構について、「類似した戦略をもつ種が類似した環境に出現する」という環境フィルタリングが注目されている。片淵君は、世界で最も樹木の多様性の高い地域であるマレーシア・サラワク州の熱帯雨林のフタバガキ科を対象として、樹木の機能形質を用いて戦略を定量化することで、熱帯樹木群集の群集形成と群集動態における環境フィルタリングの働きを詳細に検証し、3章の論文にまとめた。

第1章では、樹木群集では、環境フィルタリングが正の密度依存効果として検出されるのに対して、同種密度依存的な死亡率（負の密度依存効果）も働くことが知られていることに注目し、両者を分離して解析することに成功した。その結果、同種個体数と生存率が、2つのメカニズムの複合を示唆する二次曲線で近似でき、87%の個体は回帰線の頂点に至るよりも少ない同種個体数で生育すること、個体数が多い種が強い負の密度依存効果を受けていることを見出した。この結果は、熱帯雨林の多様性を維持する上での、負の密度依存効果の役割を強調するものである。

第2章では、環境フィルタリングの効果が、実際にどのような環境要因によってもたらされるのかを、複数のヌルモデルを組み合わせることで、定量的に示した。対象とした9個の機能形質のうち7個の形質がランダムから予測されるよりも収斂しており、明確な環境フィルタリングの検出に成功した。また土壌養分環境がその他の環境要因よりも環境フィルタリングの働きを担っていることが示した。これらの結果は、環境フィルタリングが機能する環境条件や機能形質を具体的に示した研究として先駆的なものである。

第3章では、環境フィルタリングにより、群集レベルの形質の平均値の相関が強くなると予測し、シミュレーションを行った結果、10組のうち8組の形質では環境フィルタリングを仮定すると形質平均値同士の相関が強くなった。また、多くの場合で観察値の形質平均の相関が期待されるよりも強いことを見出した。この結果は、種組成のみではなく、個体数分布にも環境フィルタリングが作用していることが示唆するもので、この分野の新しい方向性を示すものである。

これらの研究は、著者が自立して研究活動を行うに必要な、高度の研究能力と学識を有することを示している。従って、片淵正紀提出の論文は、博士（生命）の学位論文として合格と認める。